PROC. ENTOMOL. SOC. WASH.
91(4), 1989, pp. 497–501

HOMOLOGIES IN WING VENATION OF PRIMITIVE DIPTERA AND MECOPTERA

George W. Byers

Department of Entomology, The University of Kansas, Lawrence, Kansas 66045.

Abstract.—On the basis of evidence from tracheation of wing veins, distribution of macrotrichia on veins, corrugation of the wing, and comparison of wings of Diptera to those of Mecoptera, the media is four-branched and the anterior cubitus is unbranched.

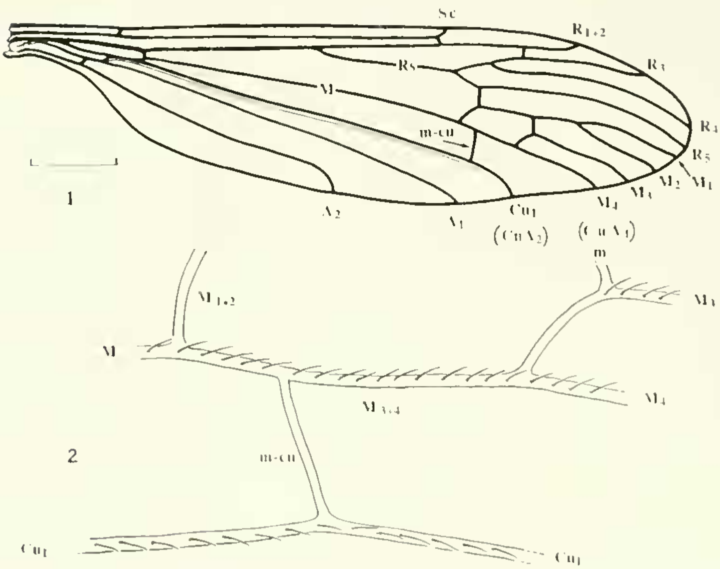
Key Words: wing venation, Tipulidae, Tanyderidae, Mecoptera

Dipterists are concerned with the interpretation of wing venation because they use venational consistencies and differences for recognition of taxa at all levels. Accordingly, it is awkward that conflicting views of venational homology are currently in use. In this paper, support is offered for one of those interpretations.

J. H. Comstock and J. G. Needham produced the most widely accepted system of nomenclature and homologies of wing veins of insects (Comstock 1918). Familiar to most entomologists, it need not be reviewed in detail here. In diagramming the hypothetical primitive or generalized insect wing, Comstock and Needham noted that alternating veins are elevated or convex (+), or depressed, concave (−) with respect to the plane of the wing. This corrugation, or fluting, had been pointed out earlier by Adolf (1879) and Redtenbacher (1886): the costa is +, the subcosta strongly −, anterior branch of the radius strongly +, the sector (Rs) and its branches −, anterior media + (but absent in extant orders of insects), posterior media and its branches −, anterior cubitus +, posterior cubitus −, and so on. K. G. A. Hamilton (1971: 429) noted that much of the fluting seen in wings of Paleoptera is reduced in wings of Neoptera, except in the costal area (C, Sc and R_1) and along the cubitus. Nevertheless, the relative elevation and depression of veins can in most cases be readily determined.

The problem with which I am concerned involves the branching of the posterior media (M) and the anterior cubitus (Cu_1). Comstock and Needham determined that vein M primitively was dichotomously four-branched, M_1, M_2, M_3 and M_4, all concave, reaching the wing margin. They believed that Cu was primitively two-branched rather near its base, with the anterior cubitus (Cu_1) being strongly convex and the posterior branch (Cu_2) concave. Vein M_{3+4} or M_4 is, in their system, connected to Cu_1 by the m-cu cross-vein. The anterior cubitus may itself be divided into Cu_{1a} and Cu_{1b} (see Snodgrass 1935: 216).

A problem arose for Comstock and Needham with the observation that what appeared to be the posterior branch of M was moderately to strongly convex in Diptera. Since all branches of M were supposed to be concave, they initially said that this vein is either an anterior branch of the anterior cubitus (Cu_{1a}) or Cu_{1a} + M_4. Their eventual conclusion, however, was that in Diptera the media has only three branches and that this convex vein is a branch of the cubitus; that is, M_4 is always absent in wings of Diptera.



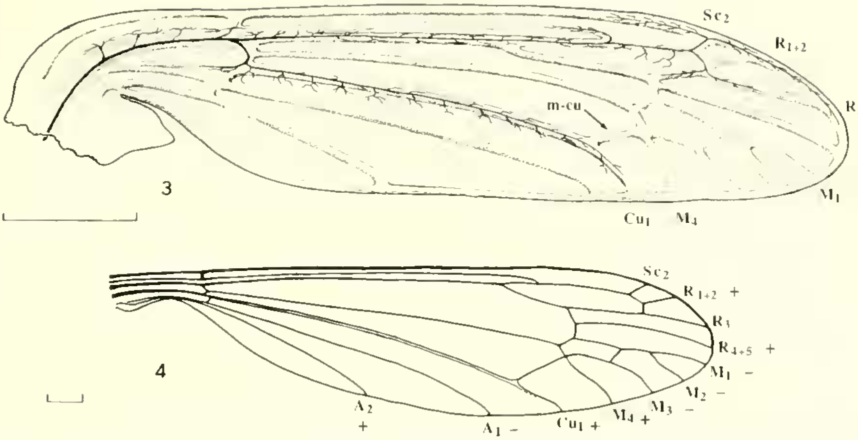
Figs. 1–2. *Pseudolimnophila inornata* (Osten Sacken). 1. Wing with venation labelled according to the Alexander-Tillyard system, with branches of M and Cu also labelled (in parentheses) according to the Comstock-Needham system. 2. Portion of venation showing distribution of macrotrichia on certain veins. Scale line = 1 mm.

This interpretation was challenged only eight years later, by R. J. Tillyard (1926), who declared that M is four-branched in flies and that Cu_1 is unbranched. Almost simultaneously, C. P. Alexander had reached the same conclusion, based on his study of Tipulidae and other primitive Diptera (e.g., Tanyderidae). A student of Comstock at Cornell University and at first a follower of the Comstock system (from 1919 to 1925), Alexander became convinced that the media has in Tipulidae four branches, as in the hypothetical, generalized pattern, and that what he had been calling the "anterior deflection of Cu_1" in crane flies was really the m-cu cross-vein.

The Alexander-Tillyard interpretation has also been widely accepted, perhaps in part because it holds that M in primitive Diptera (that is, Diptera in which the venation is not greatly reduced or modified) has the form that Comstock and Needham claimed for primitive insects generally. This view was followed, for example, by D. H. Colless and D. K. McAlpine (1970) in "The Insects of Australia." In contrast, the "Manual of Nearctic Diptera" (J. F. McAlpine et al. 1981) adopted the Comstock-Needham interpretation. Figure 1 illustrates these conflicting interpretations of M and Cu_1 in the wing of a crane fly.

The problem is basically this, I think: Is the vein (labelled m-cu in Fig. 1) connecting what appears to be the posterior branch of M with Cu_1 in fact a cross-vein, or is it the basal part of a branch of Cu_1? What kinds of evidence can be obtained to support one interpretation or the other?

Some similar problems have been solved by examination of tracheal branching. In Diptera, however, the veins are already clearly established in the pupal wing (the wing sheath) before tracheae enter the wing. In crane flies of the genus *Tipula* (Fig. 3), one trachea enters the radius and branches at the arculus, one branch continuing along the radius and through R_1 to the stigmal area, the other proceeding along the cubitus (Cu_1). In several pupae of *Tipula trivittata* Say examined (and in a few of other species), the cubital trachea did not give off any branch into the vein in question (which I call m-cu). In some individuals, perhaps preserved too soon, the trachea stopped be-

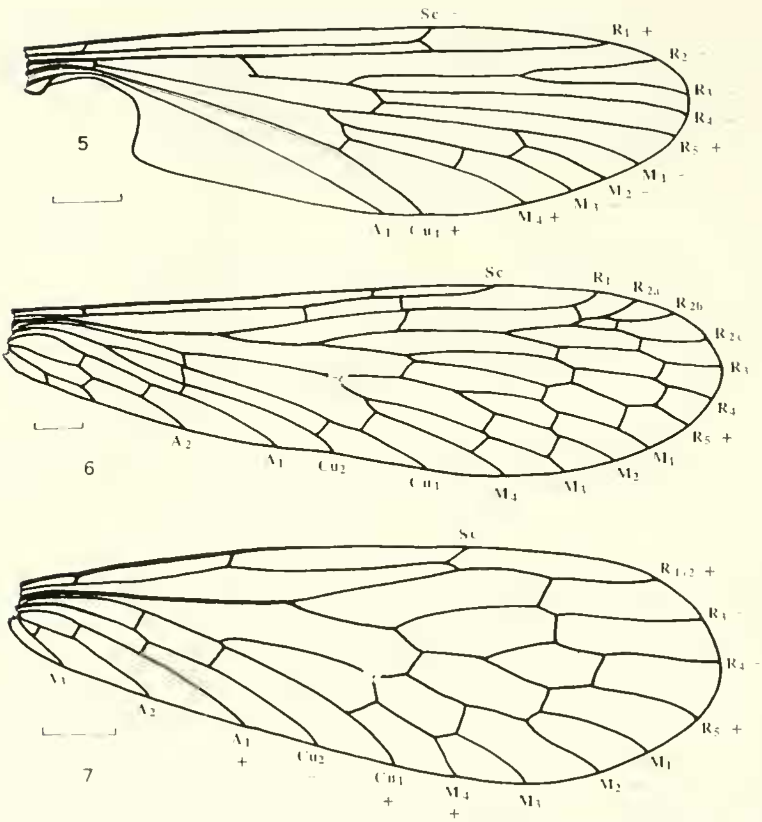


Figs. 3–4. *Tipula trivittata* Say. 3. Pupal wing (wing sheath) showing complete, slightly raised venation (shaded) and tracheal branches chiefly in R_1 and Cu_1. 4. Wing, indicating the convexity (+) or concavity (−) of certain veins. Scale lines = 1 mm.

fore reaching m-cu; in others, it passed m-cu without branching. In one specimen of *Tipula ignobilis* , however, a short branch entered m-cu for about one-fourth of the length of that vein. I find this evidence interesting but ambiguous.

A few morphologists and taxonomists have observed that, in various taxa, macrotrichia occur on certain longitudinal wing veins but not on cross-veins. This contrast is easily seen in Mecoptera, for example. Numerous individuals of several genera of Tipulidae (in all three subfamilies) were inspected with this in mind. While macrotrichia usually occur on both M and its branches and on Cu_1, although often only sparsely, they are almost never seen on m-cu. One or two machrotrichia were found on the cubital end of m-cu in a very few individuals. *Pseudolimnophila* illustrates well the contrasting presence of macrotrichia on M and Cu_1 and absence from m-cu (Fig. 2). But macrotrichia are absent as well from the basal, cross-vein-like portions of M_{1+2} and M_3, so this evidence may not be very convincing.

Homology of veins from one order to another has been determined largely by the previously mentioned corrugation, or fluting. As a general observation, two main longitudinal veins—R_1 and Cu_1—are ordinarily strongly convex in virtually all neopterous orders of insects. Such primitive flies as *Tipula* (Tipulidae) and *Protoplasa* Tanyderidae) show this condition (Figs. 4, 5). In both, a strongly concave, darkened line closely paralleling the convex Cu_1 but not reaching the wing margin has been interpreted as Cu_2 or the cubital fold, lying in the cubital furrow. Also in both, the vein that I suppose is M_4 is clearly convex, while m-cu is much less so and may be neither + nor −. But I cannot accept the view of Comstock and Needham that the convexity of "M_4" must be interpreted as this vein's being a branch of Cu_1. My reason is this: In all crane flies and tanyderids examined, vein R_5 or the combined R_{4+5} is moderately to strongly convex, while the expectation is that it should be concave. Comstock and Needham, who held that the branches of the radial sector are concave, apparently took no notice of this inconsistency. W. Hennig (1969: 311,376) did, and suggested that the apparent R_5 could include a remnant of the convex anterior media. However, it is generally accepted, I think, that the anterior media is absent in all modern orders of insects. My interpretation of the convexity of both R_5 and M_4 is that there is a structural "need" for corrugation to give some relative rigidity and strength to the respective parts



Figs. 5–7. Wing venation, showing the convexity (+) or concavity (−) of certain veins. 5. *Protoplasa fitchii* (Osten Sacken) (Diptera:Tanyderidae). 6. *Panorpa communis* Linnaeus (Mecoptera:Panorpidae). 7. *Nannochorista neotropica* Navás (Mecoptera:Nannochoristidae). Scale lines = 1 mm.

of the wing (which are otherwise rather plane). I have no idea whether this is so; but the point is that a convex M_4 is no more remarkable than a convex R_5, and no less to be expected.

Occasionally, in local populations, one finds numerous individuals that have the branches of M variously dislocated (Byers 1961). Such aberrations appear to have a genetic basis (cf. Laven 1957). While the apparent M_4 is involved in these dislocations, although less so than M_{1-3}, and even m-cu may be affected, the anterior cubitus is not. This suggests that there are, to some extent, different factors influencing the development of M and Cu_1.

Finally, there is the evidence from comparative anatomy, which is more convincing to me than any of the evidence already cited. A survey of the orders of insects to determine the most likely origin of the Diptera leads us quickly to the Mecoptera. This order, the fossil record of which goes back to the lower Permian, displays the combination of characters most closely resembling that found in primitive Diptera—characters of general body structure, external genitalia of both sexes, antennae, mouthparts and wing venation. Accordingly, we may gain from examining the branching of the media and cubitus in Mecoptera some understanding of equivalent venation in Diptera.

Comstock and Needham thought that the venation in *Panorpa* (Fig. 6), a common genus of Mecoptera, agreed with their generalized plan, that is, Rs with four branches, M with four and Cu separated basally into Cu_1 and Cu_2, but Cu_1 with no further branching. In the medial field, the venation of *Panorpa* is strikingly like that of the tanyderid *Protoplasa* (compare Figs. 6 and 5), with the same convexity and concavity of corresponding veins. Cu_2 in Tanyderidae, as in Tipulidae, is only weakly developed as a dark line in the cubital furrow behind Cu_1.

Among the Mecoptera, *Nannochorista* (Fig. 7) is most like the Diptera; the head and mouthparts are not elongated as in most Mecoptera, the mandibles are reduced in the adult, and, in wing venation, M is fused basally with Cu_1. In this genus, as in Mecoptera generally, the anterior cubitus is unbranched. Moreover, in all Mecoptera the veins R_5 and M_4 are both distinctly convex, as in the primitive Diptera.

From the evidence presented, I conclude that in the Tipulidae (probably the most primitive family of extant Diptera) and in the Tanyderidae (which I consider also very primitive flies, although their phylogenetic position is still disputed) the media (M) typically has a dichotomous division, each branch again dividing dichotomously, hence four terminal branches. Further, I conclude that the anterior cubitus (Cu_1) in primitive Diptera, at least, is *not* branched.

There is great variation in the branching and the basal fusion of veins in the order Diptera. I have not studied this in detail. Nevertheless, I find the interpretation of venation based on the Tipulidae and Tanyderidae, and compared to that of the Mecoptera, as reasonable as any other for all Diptera. An unbranched Cu_1 could be thought of as one more character linking Mecoptera and Diptera (as Antliophora of Hennig, or Mecopterida of Boudreaux) and differentiating this group (which also includes the Siphonaptera) from the Amphiesmenoptera, or Trichopterida.

ACKNOWLEDGMENTS

I thank Mr. Bryan N. Danforth for his help in rearing pupae of *Tipula* and preparing their wings for study and in verifying the patterns of corrugation of veins in various genera. Charles D. Michener and Fenja Brodo read an early version of this paper and made useful suggestions.

LITERATURE CITED

Adolf, G. E. 1879. Über Insektenflügel. Nova Acta Leop. Carol. 41: 215–291.

Boudreaux, H. B. 1979. Arthropod Phylogeny with Special Reference to Insects. John Wiley & Sons, New York. 320 pp.

Byers, G. W. 1961. The crane fly genus *Dolichopeza* in North America. Univ. Kansas Sci. Bull. 62: 665–924.

Colless, D. H. and D. K. McAlpine. 1970. Diptera, pp.656–740. *In* Waterhouse, D. F., et al., The Insects of Australia. Melbourne Univ. Press, Carlton, Victoria. xiii + 1029 pp.

Comstock, J. H. 1918. The Wings of Insects. Comstock Publishing Co., Ithaca, New York. 430 pp. (based upon a series of papers by Comstock and J. G. Needham, 1898–1899, on "The Wings of Insects," in the American Naturalist).

Hamilton, K. G. A. 1971. The insect wing, part I. Origin and development of wings from notal lobes. J. Kansas Entomol. Soc. 44:421–433.

Hennig, W. 1969. Die Stammesgeschichte der Insekten. W. Kramer & Co., Frankfurt am Main. 436 pp.

Laven, H. 1957. Vererbung durch Kerngene und das Problem der ausserkaryotischen Vererbung bei *Culex pipiens*. I. Kernvererbung. Zeitschr. Indukt. Abstammungsund Vererbungslehre 88:443–447.

McAlpine, J. F. 1981. Morphology and terminology—adults, pp. 9–63. *In* McAlpine, J. F., et al., Manual of Neartic Diptera. Vol. 1. Monogr. 27, Res. Branch, Agriculture Canada. 674 pp.

Redtenbacher, J. 1886. Vergleichende Studien über das Flügelgeäder der Insekten. Ann. K. K. Natur. Hofmus. 1: 153–232.

Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Book Co, New York. 667 pp.

Tillyard, R. J. 1926. The Insects of Australia and New Zealand. Angus and Robertson, Sydney. 560 pp.